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RESEARCH ARTICLE

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# Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores

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## Abstract

1. Forests are being converted to agriculture throughout the Afrotropics, driving declines in sensitive rainforest taxa such as understorey birds. The ongoing expansion of cocoa agriculture, a common small-scale farming commodity, has contributed to the loss of 80% rainforest cover in some African countries. African cocoa farms may provide habitat for biodiversity, yet little is known about their suitability for vertebrate fauna, or the effect of farm management on animal communities.
2. Here, we report the first in-depth investigation into avian diversity and community composition in African cocoa, by assembling a dataset of 9,566 individual birds caught across 83 sites over 30 years in Southern Cameroon. We compared bird diversity in mature forest and cocoa using measures of alpha, beta and gamma diversity, and we investigated the effect of cocoa farm shade and forest cover on bird communities.
3. Gamma diversity was higher in cocoa than forest, though alpha diversity was similar, indicating a higher dissimilarity (beta diversity) between cocoa farms. Cocoa farms differed from forest in community composition, with a distinctive decrease in relative abundance of insectivores, forest specialists and ant-followers and an increase in frugivores.
4. Within cocoa farms, we found that farms with high shade cover in forested landscapes resulted in higher relative abundance and richness of sensitive forest species; shady farms contained up to five times the proportion of forest specialists than sunny farms.
5. *Synthesis and applications*. Sunny African cocoa farms were less able to support sensitive bird guilds compared with shaded farms in forested landscapes. Our

findings support the notion that certain ecological and dietary guilds, such as ant-followers and forest specialists are disproportionately affected by land-use change. In light of the current push to increase cocoa production in sub-Saharan Africa, our results provide policymakers opportunities for more wildlife-friendly cocoa schemes that maximize avian diversity.

**KEYWORDS**

African bird, agroforestry, cocoa, farm management, forest cover, forest specialist, insectivore

## 1 | INTRODUCTION

Agricultural expansion is the main cause of terrestrial biodiversity loss worldwide (Newbold et al., 2015). The tropics, particularly sub-Saharan Africa, have the highest risk of biodiversity loss due to limited coverage of protected areas, low conservation spending and high agricultural growth (Kehoe et al., 2017). With agricultural demands projected to double in the next decades (Tscharntke et al., 2012), there is an urgent need for strategies that will combine agricultural production and biodiversity conservation. Trade-offs exist between agricultural production and biodiversity conservation, yet these aims need not be mutually exclusive: high-yield food production and high biodiversity are able to coexist in tropical smallholder agroforestry systems, in which agricultural crops are grown among shade trees (Clough et al., 2011; Perfecto & Vandermeer, 2010; Priess et al., 2007).

Cocoa is the fastest expanding export-oriented crop in the Afrotropics (Ordway et al., 2017), driven by a booming market in Europe (Squicciarini & Swinnen, 2016). Cocoa cultivation has caused mass deforestation in countries such as Ivory Coast, where it is now grown industrially in full-sun monocultures because of lack of forest land (Maclean, 2017). In other countries such as Cameroon, the 5th top exporter of cocoa worldwide, it is grown in a less intensive manner, usually under a thick forest canopy (Rice & Greenberg, 2000). Though short-term yields may be higher in full-sun plantations, shaded cocoa farms have a longer productive life span and suffer lower pest burdens, making long-term yields comparable (Tscharntke et al., 2011). However, the Government of Cameroon aims to triple cocoa production by 2035 (Ordway et al., 2017), which may lead to clearing of forested land for monocultures and conversion of shade-grown cocoa to sun monocultures (Andres et al., 2016; Schroth & Harvey, 2007).

Cocoa agroforestry systems often maintain a high diversity of rainforest shade trees that may resemble the rainforest they replaced (Bisseleua et al., 2013; Sonwa et al., 2007). Partly due to this, several studies have suggested that cocoa agroforestry systems contain considerably higher biodiversity than intensive cocoa plantations (Bhagwat et al., 2008; Bisseleua et al., 2009; Tscharntke et al., 2011; Vergara & Badano, 2009). However, most studies on cocoa are from the Neotropics and South-East Asia. In their meta-analysis, De Beenhouwer et al. (2013) highlight a lack of research on the capacity of African cocoa agroecosystems to maintain biodiversity. Specifically, we know little regarding vertebrate communities, and how they are affected by farm management practices (Schroth & Harvey, 2007; Sekercioglu, 2012). The notable exceptions are Waltert et al. (2005) and Kupsch et al. (2019), who surveyed birds across a gradient of land-use intensification which included some cocoa plots, and found that although species richness did not decrease with increasing habitat modification, community composition was significantly affected, with a decrease in abundance of large-bodied frugivores and terrestrial insectivores.

Factors affecting animal diversity in cocoa agroforestry systems occur at two spatial scales: farm level (0.25–5 Ha) and landscape level. Within the farm, management actions such as shade tree removal and pruning will affect an animal community. In the Neotropics, farms with dense, structurally diverse vegetation have been shown to support a higher diversity of birds (Cassano et al., 2009), ants (Philpott et al., 2006) and amphibians (Deheuvels et al., 2014). At a landscape scale, animals are affected by habitat connectivity as has been shown in Brazil where farms in forested areas support higher diversity of birds, bats and frogs than farms in disturbed non-forested landscapes (Cassano et al., 2009; Faria et al., 2006).

Birds are good indicators of habitat quality (Kupsch et al., 2019), with groups such as insectivores showing high sensitivity to habitat degradation (Karp et al., 2011; Powell et al., 2015; Stratford & Stouffer, 2013; Tchoumbou et al., 2020; Wolfe et al., 2015). In the tropics, many bird species depend strictly on microhabitats often only present in pristine forest (forest specialists; Stratford & Stouffer, 2013). Here we focus attention on two additional sensitive guilds of birds: ant-followers and mixed-flock species. Ant-followers are birds that pursue army ants, consuming the invertebrates flushed by the swarm (Peters & Okalo, 2009). Ant-followers are vulnerable to habitat degradation, and they are often the first guild to disappear with habitat conversion (Peters et al., 2008; Peters & Okalo, 2009). Also sensitive to habitat disturbance are mixed-species flocks, assemblages of birds of different species that move through the forest together foraging (Cordeiro et al., 2015).

In this study, we investigated the diversity of ecological bird guilds in African cocoa farms using a dataset collected over 30 years of bird mist-net captures across Southern Cameroon and Equatorial Guinea. We contrasted avian diversity and community composition

patterns between forest and cocoa across varying shade and forest cover. Specifically, we asked the following questions: (a) Are bird communities in cocoa farms less diverse than in the forest? (b) Is bird community composition different between forest and cocoa? (c) How do shade and forest cover influence bird communities in cocoa farms?

## 2 | MATERIALS AND METHODS

### 2.1 | Bird mist-net captures

We considered bird mist-net captures from Cameroonian cocoa farms and mature forest, and from one mature forest site in Equatorial Guinea, between 1990 and 2020 (see Appendix S1). These data were collected for a range of projects, and therefore did not have a standardized methodology or sampling effort. However, the similarities in the overall approach made the data comparable: at each site, we set up 12 to 20 12 × 3 m mist-nets (30-mm mesh) for 6–11 hr per day (~6:30 to 12.30–17:30; Jarrett et al., 2021; Smith et al., 2005). Nets were set up either in a straight transect or in two smaller transects. The number of sampling days per site varied (Appendix S1). We used two methods to account for this unstandardized sampling effort: (a) For diversity analyses, we sampled a standardized number of captures and sites ($n$ = 25 sites per habitat type, $n$ = 30 captures per site) and (b) for community composition analyses, we considered only relative abundance and species richness of foraging guilds, calculated for each sampling unit by dividing the number of captures or species of each foraging guild by total captures or species.

We excluded individual birds that were not identified to species level, except for the commonly caught genera *Criniger*, *Phyllastrephus* and *Terpsiphone*. The resulting database consisted of 9,566 birds captured across 83 sites (26 forest and 57 cocoa; Figure 1; Appendix S1). We used the Handbook of the Birds of the World (del Hoyo et al., 2019) to classify each species according to its primary food type, its foraging guild and whether it was a forest specialist. Species could belong to more than one category (e.g. insectivorous and forest specialist; Appendix S2). Additionally, we determined the conservation status of each species (IUCN, 2020) and whether they were geographically restricted to the Congo Basin area (Appendix S2).

We considered sampling sites independent if they were separated by at least 500 m, those separated by less were pooled. The mature forest sites were at least 1 km from forest edge, had a closed canopy and were considered largely undisturbed by logging activity. Sites were classified into three regions: south, ecotone and west, corresponding to distinct ecoregions in Cameroon (Tamungang et al., 2014). We assigned each sampling visit to a season, either wet or dry, according to rainfall patterns of the corresponding region (Molua, 2006).

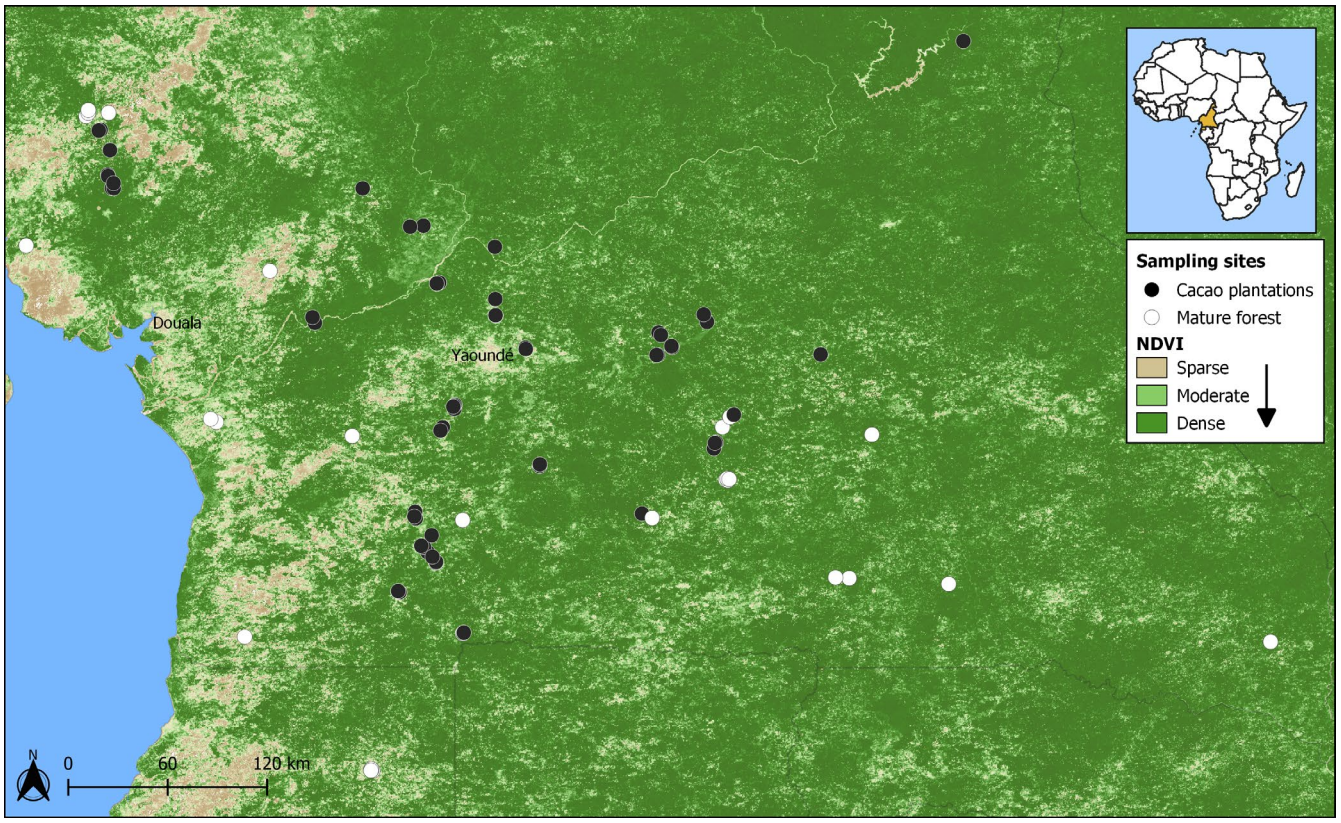


**FIGURE 1** Map of all mature forest (white) and cocoa (black) sample sites across Southern Cameroon and Northern Equatorial Guinea. The base map shows eMODIS Normalized Difference Vegetation Index (NDVI; October 2018), as an indicator of vegetative land cover (accessed from https://earlywarning.usgs.gov/)

## 2.2 | Quantifying diversity

We quantified diversity using Reeve et al.'s (2016) framework implemented in the package RDIVERSITY (Mitchell et al., 2020), which measures components of alpha, beta and gamma diversity over a continuum of viewpoint parameters, $q$ (for details see Allen et al., 2019; Kirkpatrick et al., 2018; Kumar Sarker et al., 2019). The value of $q$ determines the relative importance attributed to species of differing rarity, giving less importance to rare species as $q$ increases (Appendix S3). Here, we used $q = 0$, 1, 2 and $\infty$ as they align with commonly used diversity metrics (species richness, Shannon entropy, Simpson diversity and Berger Parker diversity). The framework considers a metacommunity composed of multiple subcommunities, each containing a number of species (Appendix S3). From the framework we calculated, metacommunity gamma diversity, subcommunity gamma diversity, subcommunity alpha diversity and representativeness of subcommunities within the metacommunity (a type of beta diversity; Appendix S4). Representativeness takes a value between 0 and 1; it is smallest when species present in each subcommunity are not present elsewhere in the metacommunity, and largest when all species in the metacommunity are present in the subcommunity (Appendix S3; Reeve et al., 2016).

We standardized number of sites ($n = 25$ per habitat type) and number of captures ($n = 30$ per site) for beta and gamma diversity measures. For alpha diversity, we standardized number of captures per site ($n = 30$) but included all sites, as this measure was calculated for each site in isolation and therefore was not affected by the number of sites. We then repeated each analysis 50 times. We excluded any sites below the capture threshold. We chose this number of individuals as it allowed us to maximize the number of captures while preserving the greatest number of sites. Diversity measures displayed in our results section are an average across the iterations. To improve robustness of our results for subcommunity alpha, we interpolated to 30 captures and extrapolated to 200 captures using the package iNEXT (Hsieh et al., 2016; Appendix S3). We conducted all analyses in R version 3.6.3 (R Core Team, 2020).

## 2.3 | Shade and forest cover measurements

We investigated the effects of forest cover on birds in a subset of cocoa farmssek ($n = 28$) for which we had canopy measurements. We considered the following spatial scales of forest cover: cover of the farm itself (~1.5 Ha; henceforth shade cover) and mean forest cover in a 1.4, 2.5 and 4 km radius surrounding the farm (henceforth forest cover; Appendix S3). Shade cover was an indication of how intensely the farm was managed; traditional or shade farms preserved a mostly intact forest canopy, while in intensive or full-sun farms, shade trees were cut exposing cocoa trees to sunlight. Forest cover was a measure of how degraded the landscape was surrounding the farm.

To measure shade cover, we took photographs at 10 locations in each farm, spaced out by 24 m and at minimum 50 m from farm edge. We took photographs using a camera with a fish-eye lens on an extendable pole (12 m). Using the software ImageJ (Schneider et al., 2012), we converted the photographs to black and white, and then calculated the percentage of black (vegetation) in each photograph. The shade cover value used was a mean of the 10 pictures. To measure forest cover, we used the percent tree cover layer of the MODIS Vegetation Continuous Fields (MOD44B; Dimiceli et al., 2011), which is published yearly and has a resolution of 250 m. We downloaded the MOD44B layer corresponding to 2018 (birds were captured 2017–2020). In QGIS 2.18.23 (QGIS Development Team, 2018), we created a 1.4, 2.5 and 4 km radius buffer around each farm and extracted the mean percentage tree cover from the pixels within the buffer (Appendix S3). Shade cover measurements ranged from 19.6% in the most intensively managed farm to 98.7% in the least, and forest cover ranged from 9.0% in an urbanized area to 65.8% in a farm adjacent to a forest reserve.

## 2.4 | Data analysis

We used GLMMs with a binomial distribution to investigate the differences in bird community between forest and cocoa, and to investigate the effect of shade and forest cover on bird community composition in the subset of 28 farms for which we had canopy cover data. We grouped visits to a site in the same season and year into one sample unit. We used relative abundance and relative species richness as response variables to allow for varying sample size. For the comparison between cocoa and forest, full models contained an interaction term between season and habitat (forest or cocoa), a fixed effect for region and random factors for site and year. For the cocoa shade and forest cover analyses, full models contained fixed effects for shade cover, forest cover and season, and random effects for site and year. Here we present results for the largest buffer size (4 km radius), which was overall the best predictor of bird community composition (but see Appendix S3 for model selection and full results). We performed backwards model selection using likelihood ratio tests on fully nested models (LRTs, cut-off probability $p > 0.05$), until reaching a minimal adequate model.

We used minimal adequate models to estimate coefficients; we report estimates and 95% confidence intervals. All GLMMs were ran using the package GLMMTMB (Brooks et al., 2017) in R.

# 3 | RESULTS

## 3.1 | Bird diversity in cocoa plantations and mature forest

Metacommunity gamma diversity was higher in cocoa than in forest, though the difference became smaller at increasing values of $q$ (Figure 2a). At $q = 0$, gamma diversity in cocoa was 90.0 and in

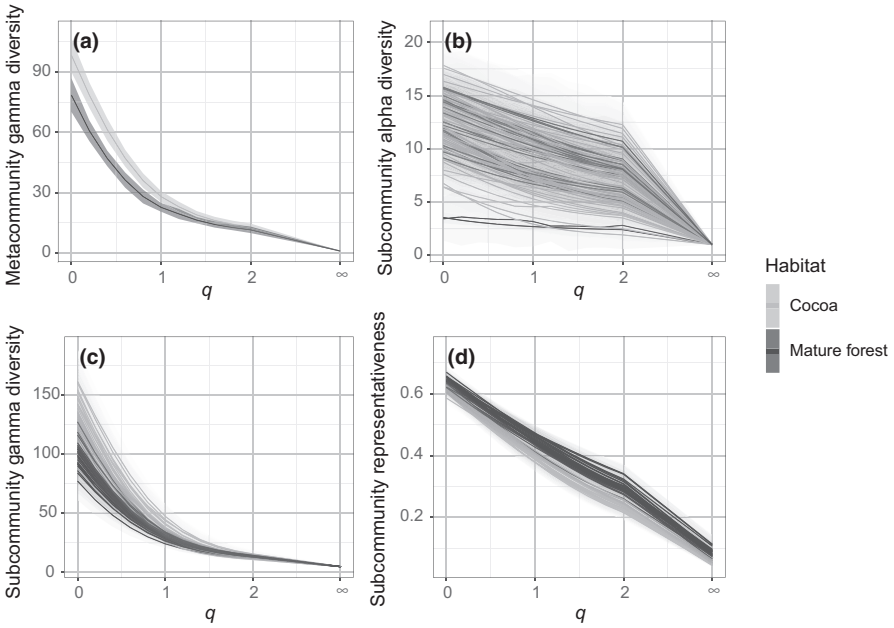


**FIGURE 2** Measures of diversity in cocoa and mature forest sites across varying values of *q*: (a) Metacommunity gamma, (b) Subcommunity alpha, (c) Subcommunity gamma and (d) Subcommunity representativeness (a type of beta diversity; see Reeve et al., 2016). Measures of gamma and beta diversity were calculated over $n = 25$ sites per habitat type and $n = 30$ captures per site, and alpha diversity was calculated for $n = 30$ captures per site. Shaded areas represent 95% confidence intervals derived from the 50 iterations of the analyses

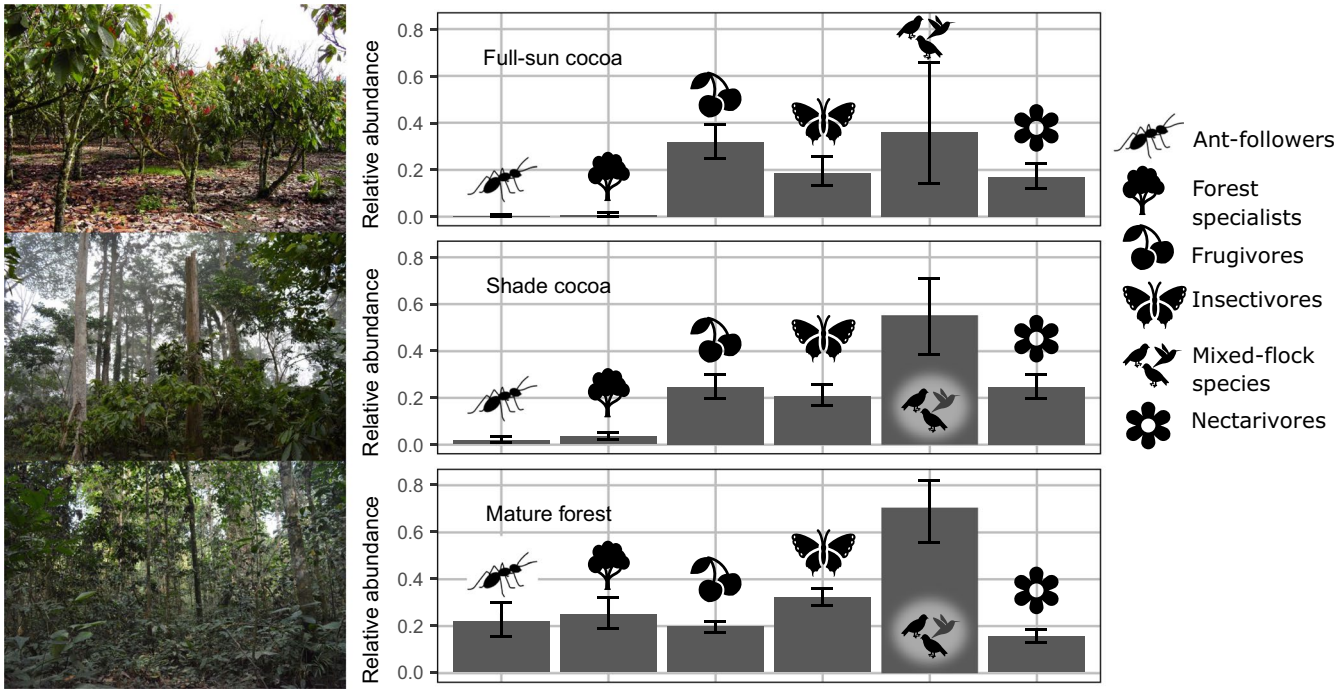


**FIGURE 3** Relative abundance foraging guilds in full-sun cocoa (20% shade cover), shady cocoa (90% shade cover) and mature forest. Shaded bars and error bars represent the fitted values and 95% confidence intervals from the minimal adequate models. Top photograph: photo by Bea Maas—used with permission

forest 71.0, and at $q = 2$ it was 12.8 in cocoa and 11.5 in forest. Subcommunity alpha diversity was similar between cocoa and forest across all values of *q*; after 30 captures at $q = 0$ cocoa reached 12.4 species and forest reached 12.2 species (Figure 2b). Subcommunity gamma diversity was higher in cocoa than forest at low values of *q*, but became similar as *q* increased (Figure 2c). At $q = 0$, subcommunity gamma in cocoa was 136.7 and in forest 100.2. Subcommunity representativeness was consistently lower in cocoa than in forest over all values of *q*; at $q = 0$ representativeness in cocoa was 0.61 and in forest 0.64 (Figure 2d).

### 3.2 | Community composition in cocoa plantations and mature forest

Bird communities in cocoa and forest differed in their composition (Figure 3; Table 1; Appendix S5). Habitat was a significant variable in explaining the relative abundance of insectivores, forest specialists, ant-followers and mixed-flock species; these groups constituted a smaller proportion of all captures in cocoa farms than in forest. The largest effect size was for forest specialists that made up 25% of captures in forest and 3% in cocoa. Frugivores

**TABLE 1** Relative abundance and species richness of feeding guilds in cocoa and mature forest as predicted by minimal adequate models

| | | Cocoa | | | Forest | | | Dry | | | Wet | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Type of analysis** | **Response guild** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** |
| Abundance | Insectivores | 0.2[a] | 0.19 | 0.23 | 0.32 | 0.28 | 0.36 | | | | | | |
| | Forest specialists[b] | 0.03 | 0.02 | 0.04 | 0.25 | 0.18 | 0.32 | 0.04 | 0.03 | 0.06 | 0.06 | 0.04 | 0.08 |
| | Nectarivores[c] | 0.18 | 0.16 | 0.21 | 0.15 | 0.13 | 0.18 | | | | | | |
| | Mixed-flock species | 0.49 | 0.40 | 0.58 | 0.70 | 0.56 | 0.82 | | | | | | |
| | Frugivores | 0.28 | 0.25 | 0.31 | 0.19 | 0.17 | 0.22 | 0.24 | 0.21 | 0.27 | 0.27 | 0.25 | 0.30 |
| | Ant-followers | 0.03 | 0.02 | 0.04 | 0.24 | 0.18 | 0.31 | | | | | | |
| Species richness | Insectivores | 0.30 | 0.29 | 0.33 | 0.41 | 0.38 | 0.43 | | | | | | |
| | Nectarivores | 0.18 | 0.16 | 0.21 | 0.15 | 0.13 | 0.18 | | | | | | |
| | Frugivores | 0.22 | 0.20 | 0.24 | 0.11 | 0.09 | 0.13 | | | | | | |
| | Ant-followers | 0.11 | 0.10 | 0.13 | 0.26 | 0.23 | 0.29 | | | | | | |
| | | **Cocoa** | | | | | | **Forest** | | | | | |
| | | **Dry** | | | **Wet** | | | **Dry** | | | **Wet** | | |
| **Type of analysis** | **Response guild** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** | **Estimate** | **Lower** | **Upper** |
| Species richness | Mixed-flock species[d] | 0.31 | 0.28 | 0.34 | 0.34 | 0.32 | 0.37 | 0.44 | 0.40 | 0.49 | 0.41 | 0.38 | 0.45 |
| | Forest specialists | 0.08 | 0.05 | 0.11 | 0.11 | 0.08 | 0.16 | 0.31 | 0.24 | 0.39 | 0.29 | 0.24 | 0.35 |

[a]Values displayed are the fitted values and 95% CIs predicted by the minimal adequate models. Where only habitat had a significant effect, there are two fitted values.

[b]In cases where both habitat and season had a significant effect on relative abundance, there are four fitted values.

[c]Habitat was not significant in the model predicting relative abundance of nectarivores

[d]For mixed-flock and forest specialist species richness, the interaction between habitat and season was retained in the minimal adequate model.

constituted a larger proportion of total captures in cocoa farms than in forest, and occurred in higher relative abundance in the wet season.

Relative species richness of insectivores, ant-followers, mixed-flock species and forest specialists was significantly higher in forest than cocoa (Table 1; Appendix S5). Relative species richness of frugivores and nectarivores was higher in cocoa farms. For mixed-flock species and forest specialists, the effect of season on relative species richness depended on habitat; these groups made up a larger fraction of all captures in the wet season (compared with the dry season) in cocoa, but the opposite was true in the forest.

### 3.3 | Effect of farm shade and forest cover on bird communities

Effects of shade and forest cover on bird abundance varied between guilds (Figures 3 and 4; Appendix S5). The only guild that decreased in relative abundance with increasing shade cover was frugivores, from 32% in full-sun farms to 24% in the most shaded farms. Ant-followers increased in relative abundance with both shade and forest cover; they constituted 0.2% of captures in sunny farms and 2% in shady farms, and they increased from 0.1% to 6% with increasing forest cover. Forest specialists increased in relative abundance also with shade and forest cover; shady farms had five times the relative abundance of forest specialists than full-sun farms, and their relative abundance increased from 0.7% in farms with minimum forest cover to 7% in farms with high forest cover. Neither shade cover nor forest cover had significant effects on the relative abundance of insectivores, nectarivores or mixed-flock species.

Shade cover and forest cover had no effect on the relative species richness of frugivores, nectarivores, insectivores and mixed-flock species (Appendix S5). Relative species richness of ant-followers increased significantly with forest cover; from 5% in farms with low forest cover to 18% in farms with high forest cover. Forest cover had a significant effect on the relative richness of forest specialists, increasing from 1% at low forest cover to 19% at high forest cover.

## 4 | DISCUSSION

Our study is the first to specifically examine African cocoa farms as habitat for birds. We found that sensitive guilds such as forest specialists and ant-followers represented a larger proportion of the community in shady farms compared with full-sun farms, and that these groups occurred at higher relative abundance in farms with high forest cover. In the current climate of agricultural intensification, our findings highlight the potential for farmland to

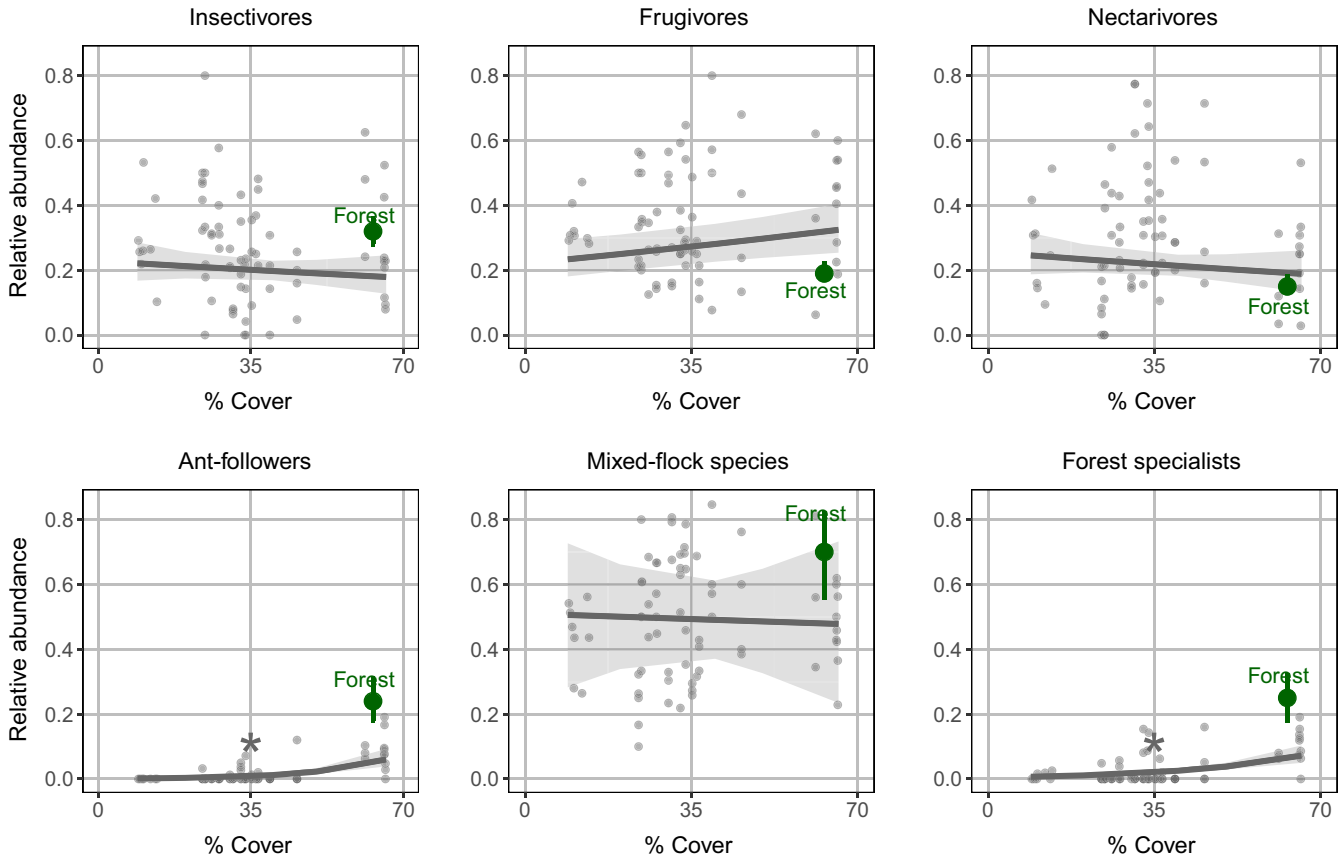


**FIGURE 4** Effect of landscape forest cover on the relative abundance of foraging guilds. The line indicates the effect size predicted by the minimal adequate model and the shading corresponds to the 95% CIs. The asterisks indicate statistical significance. The point represents the relative abundance of the corresponding foraging guild in mature forest, with associated CIs. The dots correspond to the raw data

be managed in favour of avian communities, and we provide further evidence of the importance of maintaining forested areas in the landscape.

We found that the cocoa-farms bird assemblage comprised more species than the forest assemblage. This could possibly be due to the variability of habitat characteristics in cocoa farms, which can range from full-sun scrubby plantations to shaded farms that are structurally similar to the forest (Sonwa et al., 2007; Tscharntke et al., 2011). Indeed, the lower representativeness of cocoa farms indicates that they were more dissimilar between each other compared with forest sites. These findings support Solar et al. (2015), who report increased beta diversity between secondary forest sites than between undisturbed forest sites. The authors argue that the higher between-site beta diversity of disturbed forests may attenuate species loss at a larger scale. However, though cocoa farms may contain more species that are rare across the metacommunity, these are likely not forest- or range-restricted species (Appendix S2). Indeed, there is an overall trend towards increasing generalist species in disturbed forest landscapes (Rutt et al., 2019). Therefore, while cocoa farms may play a role in the conservation of certain bird guilds, we must also prioritize protection of undisturbed primary forests that provide habitat for specialized species that do not frequently occur in modified habitats (Stratford & Stouffer, 2013; Tscharntke et al., 2011).

Our results support Waltert et al. (2005), who found that species richness in Afrotropical forest did not differ between mature and agroforest. However, other studies showed different patterns. For example, Reitsma et al. (2001) found lower alpha and gamma diversity of birds in Costa Rican forest compared with managed cocoa, yet De Beenhouwer et al. (2013) found an 11% decrease in bird species richness from forest to agroforestry. Importantly, the diversity patterns we observed were affected by the *q* value. At higher values of *q*, gamma diversity became similar between forest and cocoa, indicating that both habitats contained a similar number of abundant species. Clear examples in forest were Fire-crested Alethe *Alethe castanea* and Yellow-lored Bristlebill *Bleda notatus*, two forest specialist species, that made up a considerable fraction of the community in almost all forest sites. Our results demonstrate how conclusions about diversity can change depending on the measurement parameters. We argue that using a range of metrics and *q* values gives more detailed and useful information about a community's diversity.

The broad differences in community composition that we found between cocoa farms and forest are consistent with literature from across the tropics. The shift from forest to cocoa results in a decrease in insectivores, forest specialists and ant-followers and an increase in frugivores and nectarivores in the Neotropics (Faria et al., 2006; Rice & Greenberg, 2000) and Asia (Maas et al., 2016; Marsden et al., 2006). Our findings contribute to a growing recognition that species loss in forested systems is linked to certain ecological guilds. Throughout tropical realms, distantly related species have evolutionarily converged on similar behaviours, such as ant-following and participating in mixed-species flocks, which reduce their resiliency to forest loss and habitat degradation (Powell et al., 2015).

We found that the community composition of birds in cocoa farms was significantly affected by shade and forest cover, with an increased relative abundance of forest specialists, ant-followers and mixed-flock species in shaded farms with high forest cover. Forest specialists are closely tied to vegetation structure (Powell et al., 2015; Stratford & Stouffer, 2013), especially with the understorey, which is entirely removed in intensive cocoa plantations (Kessler et al., 2005). Additionally, habitat amount (e.g. proportion of forest in landscape) is important in determining bird abundance and richness, and this effect may be more pronounced in understorey or forest specialist species (Carrara et al., 2015; De Camargo et al., 2018), explaining the increased relative abundance and diversity of these birds with forest cover. Given the current rate of land-use change, forest birds are under severe threat and will likely undergo rapid species loss (Maas et al., 2009; Powell et al., 2015; Sekercioglu, 2012).

Ant-follower abundance is driven by the abundance of swarm-raiding army ants (Peters et al., 2008; Peters & Okalo, 2009). Ants are affected by farm management: Bisseleua et al. (2009) found that ant species richness was significantly higher in structurally diverse, low-intensity cocoa systems compared with intensive systems. Additionally, ants are affected by landscape-level processes, as their sensitivity to temperature limits their ability to move between habitat patches (Rizali et al., 2013). Therefore, shaded farms in forested landscapes likely contain a community of ants like that in the forest, in turn supporting the ant-following bird population. Mixed-flocks have hardly been studied in the Afrotropics (but see Cordeiro et al., 2015; Péron & Crochet, 2009), but literature from other regions suggests that this guild is sensitive to disturbance (Goodale et al., 2015; Tien et al., 2005). Mixed-flock frequency and attendance seems to increase with vegetation density and structure, perhaps due to increased prey availability, reduced exposure to predators and protection from climatic conditions (Tien et al., 2005).

Contrary to expectations, we found no effect of shade or forest cover on relative abundance or richness of insectivorous birds. This could be driven by species such as the Chestnut Wattle-eye *Platysteira castanea* and the Paradise Flycatcher *Terpsiphone* sp., which occurred in relatively high abundances in most cocoa farms. Indeed, studies such as Waltert et al. (2005) and Sekercioglu (2012) suggest that small-bodied insectivores respond less to land-use change compared with large-bodied insectivores. From a human perspective, the presence of these small insectivores in cocoa farms could be beneficial due to their role in agricultural pest control (Karp et al., 2013; Maas et al., 2016).

In this study, we were able to see general trends in bird communities in forest and cocoa through mist-net capture data. However, given the variable sampling effort, we were only able to consider relative abundance, which may not be representative of absolute abundance. Additionally, the abundance of species' can be a misleading indicator of habitat quality as human-modified habitats can act as population sinks or ecological traps (Johnson, 2007; Robertson &

Hutto, 2006). Future studies in Afrotropical cocoa should consider demographic and morphological data to help establish the value of agroforestry systems as buffer habitat and wildlife corridors (Jarrett, Powell, et al., 2021; Schroth et al., 2004).

Our study provides strong evidence that African cocoa plantations can be of value for conserving avian diversity. However, plantations need appropriate management if habitat is to be provided for forest bird communities. Low-intensity shaded cocoa not only provides habitat for forest birds and other vulnerable taxa but can also produce high yields and farmer income, comparable to more intensive systems, thanks to lower pest burdens, longer productive life span of trees and lower input costs (Armengot et al., 2016; Clough et al., 2011; Tscharntke et al., 2011). This dual function of cocoa agroforestry systems aligns with a land-sharing perspective, in which agriculture is managed at low intensity and in favour of biodiversity. However, our results also demonstrate that even the shadiest cocoa farms are not equivalent to forest, and therefore we argue that within a land-sharing scenario there must be areas of forest preserved on the landscape. In conclusion, to prevent extreme deforestation and biodiversity loss in one of the world's diversity hotspots, policymakers should actively encourage ecologically sustainable agricultural practices such as shaded cocoa agroforestry that employs science-based management.

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## AUTHORS' CONTRIBUTIONS

C.J., T.B.S. and L.L.P. conceived the ideas and designed the methodology; C.J., T.B.S., L.L.P., T.T.R.C., D.F.F., M.T., M.N.F.E., J.W. and K.B. collected the data; R.H. and A.J.W. contributed to fundraising and logistical support; C.J. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

Data available via the Figshare Digital Repository https://doi.org/10.6084/m9.figshare.13526318.v2 (Jarrett, Smith, et al., 2021).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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